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This project attained its objectives of developing an animal model to examine the neural mechanisms of attention. The concepts and procedures were successfully produced and resulted in two publications describing the experimental strategy and the results. The last part of the project examined the role of the basal forebrain cholinergic system and its projections to the frontal cortex. This system is important for attention as assessed in the two-choice reaction time task. These results have implications for behavioral, cognitive, and neural descriptions of the mechanisms involved in attention.

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NEURAL MECHANISMS OF ATTENTION
FINAL TECHNICAL REPORT
AFOSR 89-0481

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SUMMARY

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The research project has been highly successful in reaching all of its goals. The rationale and strategy for developing behavioral tests of attention in animals was elaborated in a review chapter (Olton, et al., in press). An animal model for two-choice reaction time for rats was successfully developed, and the validity of this model was demonstrated by comparing the results of equivalent experiments with rats and humans. A manuscript describing this research has already been published (Pang, et al., 1992), and is attached in an appendix for further details. The use of this model to identify neurobiological mechanisms involved in attention has also been successful. An examination of the role of the nucleus basalis magnocellularis (NBM) and frontal cortex demonstrates that the integrity of this system is necessary for normal performance in this task. A working draft of this manuscript has already been prepared, and should be submitted for publication soon. Finally, preliminary experiments demonstrate the usefulness of this experimental strategy to address other questions in attention, both cognitive ones and neurobiological ones. Thus, in addition to the specific information about animal models of expectancy in attention and the neurobiological mechanisms underlying them, this project provides the opportunity to develop the research in many productive and important directions.

Attention: Neurocognitive Analyses.

Olton, D.S., Pang, K., Merkel, F., and Egeth, H. (in press). In Animal Cognition, T. Zentall (ed.). Hillsdale, N.J.: LEA Associates.

Both neural and cognitive systems have considerable plasticity. The same stimulus at different times may elicit different responses depending on the influence of other variables on the system. The characteristics of this plasticity differ markedly in terms of many parameters: the variables that produce it, how quickly it occurs, how long it lasts, what stimulus and response systems can be influenced, and so forth. Our investigation compares analyses of plasticity that have been conducted in the context of memory and attention, and suggests ways in which lessons learned from the analysis of the brain mechanisms

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involved in mnemonic processes can be applied to the analysis of the brain mechanisms involved in attentional processes.

The comparative approach to study cognitive processes in animals can identify general principles that may hold for the neural mechanisms of cognitive processes in several species of animals, including humans. Direct access to the human brain, both to manipulate it and measure it, is extremely limited, both in current practice and in the foreseeable future. As long as the welfare of the individual being studied is more important than the acquisition of basic knowledge (an ethical position that is so strongly developed that it is unlikely to change), information about the neural systems involved in human cognition cannot be obtained in sufficient detail to resolve fundamental issues about the relation between mind and brain. The focus of this analysis is on the use of animals to identify the general neural mechanisms involved in cognitive processes such as attention.

Several model systems have been developed to assess the neural basis of specific kinds of attention. However, no large scale integration of the neural analysis of attention has yet been undertaken. As one indicator of the difference in the maturity of neural analyses of memory and of attention, consider the presentations at the Society of Neuroscience in 1991. In the slide and poster sessions, 21 were titled "learning and memory," and these had subheadings referring to electrophysiology, anatomy, neurochemistry, and other topics. No single session was labelled "attention." In the list of keywords, many presentations had the word "learning" or "memory" listed, whereas only a few had the word "attention" listed. Presentations at the Society for Neuroscience are not the only criteria to judge the amount of work being done in a given area, but even if these data are biased for some unknown reason, they demonstrate such a substantial difference that even significant quantitative adjustments would not change the picture. The point is clear: much more research is being conducted on the neural analysis of mnemonic plasticity than on the neural analysis of attentional plasticity.

The reasons for this difference may be many, but one important difference in the study of memory and attention is the availability of experimental procedures for animals to assess attentional processes in ways that are homologous to those used in humans. In the study of attention, analyses equivalent to those for recent memory, with appropriate independent variables, psychological constructs, and ethological considerations, are still being developed. The object of our research program is to extend the analysis of attention and develop procedures that can be used for rats and that incorporate the same features used in experiments for humans. If tests of attention in humans and rats can be integrated in the same way that tests of memory have been integrated, then the rich conceptual and empirical body of information developed in the study of human attention can be applied to the study of attention

in animals, which then opens the door to an examination of the neural bases of these attentional mechanisms.

Both attention and memory provide significant plasticity in the nervous system, changing the pathways from receptors to effectors. Currently, the conceptual frameworks to describe the cognitive mechanisms involved in attention and memory are different. Compared to the substantial amount of information currently available about the neural mechanisms of memory, little information is available about the neural mechanisms of attention. What are the similarities and differences in these neural systems? The likelihood of them differing in fundamental neurobiological mechanisms, such as the flow of ions across membranes or synaptic currents, is very small. A more likely difference is in localization of function, the conjunction of neuroanatomical areas and neurochemical systems that respond to differences in attentional demands and mnemonic demands.

Comparison of the neural mechanisms of attention and memory can help develop a general cognitive/systematic/computational framework that is independent of specific experimental procedures. In both cases, the input/output functions of the nervous system have been changed by the addition of some other variable, attentional or mnemonic. Similarities and differences in neural mechanisms can help distinguish between the cognitive processes of memory and attention, unify and integrate two fields that have developed relatively independently of each other, and take the success that has characterized the neural analyses of memory and apply it to the neural analyses of attention.

Expectancy and Stimulus Frequency: A Comparative Analysis in Rats and Humans.

Pang, K., Merkel, F., Egeth, H., and Olton, D.S. Perception and Psychophysics, 1992, 51, 607-615.

Attention enables individuals to deal effectively with the tremendous amount of information that they encounter. Knowledge of the cognitive mechanisms of attention is, therefore, important for theories of information processing. Research with human subjects has led to many psychological theories of attention.

The neurobiological mechanisms of attention have been studied in humans using event-related brain potentials, positron emission tomography, and neuropsychological analysis of brain-damaged patients. However, investigations of the cellular mechanisms of attention (single cells, neurotransmitter systems, etc.) still require the use of animal models to obtain more direct access to the brain than is possible in humans. In order to assess the appropriateness of a model, animal and human studies should be directly comparable. This comparison is facilitated by

manipulating the same independent variables and measuring the same dependent variables for both humans and animals.

In the present study, we examined expectancy in rats and humans using directly comparable procedures. Choice RT tasks were performed by rats and humans, and expectancy was manipulated by varying the relative frequencies of two stimuli. We addressed three issues. 1) Does stimulus frequency influence expectancy in rats and humans in similar ways? 2) Does stimulus frequency affect expectancy for auditory stimuli, as well as that for visual stimuli? If so, are the effects of stimulus frequency similar for the two modalities? 3) What are the relative contributions of the probability effect and the repetition effect in expectancy? The comparable data we obtained for rats and humans provide evidence that the behavioral procedures described here can be used to examine the neurobiological substrates of expectancy and attention.

For the rats, the design of the operant boxes encouraged the rats to stand on their hind legs, use their forepaws to depress two levers simultaneously, and place their mouth near a water spout. Visual and auditory stimuli, levers, and water spout were positioned so that the stimuli were clearly discernible to the rat and water could be collected with minimal movement. Each trial began when the rat simultaneously pressed both levers. One of the two stimuli was presented after a variable delay. A correct response was a release of the left lever for a visual stimulus (light trials) or a release of the right lever for an auditory stimulus (tone trials). Following a correct response, the stimulus was turned off and water reinforcement was delivered. An incorrect response was a release of the right lever on light trials or a release of the left lever on tone trials. Following an incorrect response, the stimulus was turned off, the buzzer was activated for 1 s, and a 10 s time-out period ensued during which the houselight was turned off and no trials could be initiated. At the end of the time-out period, the house light was turned on and the rat was allowed to start the next trial. If the rat released both levers in response to a stimulus, the first lever release, but not the second, was recorded as correct or incorrect. A premature response was a release of any lever prior to stimulus onset; it activated a buzzer for 0.5 s and initiated a 10 s time-out period after which the trial was repeated (correction trial).

One test session, 45 - 60 minutes long, was given each day and consisted of 100 - 200 trials. The relative frequency of the two stimuli remained constant within a session, but changed from session to session. Five frequency pairs (frequency of tone/frequency of light, expressed as percentages) were presented in the following order with the 50/50 condition presented twice: 0/100, 10/90, 50/50, 100/0, 90/10, 50/50. This series was repeated in the same order throughout the study.

The human subjects had similar procedures. An IBM PC-AT

compatible computer controlled the experiment and recorded the data. The internal computer clock measured RT and delay intervals with 1 ms resolution. A home-made response box had two push button switches located 4 cm apart. The response box was connected to the computer game port. A color monitor (Princeton Graphics SR-12) with a Sigma-400 graphics card (Sigma Designs) displayed the visual stimulus, a filled light grey rectangle (8cm high x 12cm wide) in the center of the monitor screen. The rectangle subtended an angle of $11.3^\circ \times 16.7^\circ$ from a typical viewing distance of 40 cm; its luminance was 136 cd/m^2 . The luminance of the remainder of the screen was 0.22 cd/m^2 . The internal computer speaker delivered the auditory stimulus and the negative secondary reinforcer (NSR). The auditory stimulus was a 3 KHz tone with a peak amplitude of 80 Db. The NSR was a 500 Hz tone with a peak amplitude of 55 Db.

Each person was comfortably seated directly in front of the monitor, speaker, and response box in an isolated, enclosed room. The right and left index fingers of the subject rested on the right and left switches, respectively, of the response box. Each trial was initiated by pressing both buttons simultaneously. A stimulus was presented following a random interval of 1, 2 or 3 s. As with the rats, the correct response was a release of the left button for the visual stimulus and a release of the right button for the auditory stimulus. Following a correct response, the stimulus was turned off and an intertrial interval of 0.5 s began. Following an incorrect response, the stimulus was turned off, the NSR was activated for 1 s and a delay of 5 s was initiated. Following a premature response, the NSR was activated for 0.5 s and a delay of 5 s was initiated. An intertrial interval of 0.5 s followed the delays associated with the incorrect and premature responses. One test session was given each day, with 250 trials per session; each session had a single frequency condition. A total of 18 sessions (3 sessions at each stimulus frequency except the 50/50 condition which had 6 sessions) was given to each subject. No breaks were required within a session, but each subject was encouraged to rest as long as desired between trials. Each test session lasted about 15 minutes. Only data from the test sessions are reported in this paper. As in Experiment 1, data from the first 20 trials in a session were discarded.

In both rats and people, the general session effects of stimulus frequency were similar. Both species shifted response bias toward the more frequent stimulus, but did not alter stimulus discriminability. The shift in response bias was associated with a decreased RT to the more frequent stimulus in the visual modality. This pattern of results demonstrates that the frequency of previous events affects expectancy in both rats and humans.

In both rats and people, RT and errors were influenced by stimulus probability and stimulus repetition. Visual RT, visual errors, and auditory errors in rats decreased as stimulus probability or stimulus repetition increased. Auditory RT and

auditory errors in humans showed the same pattern; both decreased as stimulus probability or stimulus repetition increased. Visual errors decreased as the stimulus probability increased. The effects of stimulus probability and repetition approached significance for visual RT. These results confirm that RT and errors in human subjects depends on both stimulus probability and repetition and extend these findings to rats.

The similar results from rats and humans support the conclusion that rats can provide a useful model of human performance in expectancy tasks. Although further work is required to extend the rat model, this conclusion justifies the use of rats to identify the neural mechanisms of probability and repetition effects. Additional comparative studies can generate and validate new tasks to model other cognitive processes, such as attention.

Finally, the present experiment introduces an experimental procedure to measure two-choice RT and accuracy in rats. Although experiments have measured RT of a single response in rats, our procedure is the first that allows measurement of RT for two independent responses in rats. Because this type of procedure is so widely used in studies of human attentional processes, the development of an analogous procedure for animals can provide the opportunity to answer important questions about the cognitive and neural mechanisms involved in different types of attention.

BASAL FOREBRAIN CHOLINERGIC SYSTEM AND ATTENTION

Pang, K., Egeth, H., and Olton, D.S. Nucleus Basalis Magnocellularis and Attention. In preparation.

Cells of the nucleus basalis magnocellularis (NBM) send their axons to the cortex and terminate on cells in the cortex. This projection is important to cerebral function, both physiologically and psychologically. The NBM has been implicated in divided attention. Lesions of the NBM with ibotenic acid impaired divided attention but not focussed attention. Rats were trained to discriminate between two stimuli, each associated with a different fixed interval. Presentation of a single stimulus required that the animal attend to and time a single stimulus. These trials assessed focussed attention. Presentation of both stimuli simultaneously on a trial required that the animal attend to and time both stimuli simultaneously. These trials assessed divided attention. Normal rats able to time both stimuli when presented singly or together, thus, demonstrating good focused and divided attention. Rats with NBM lesion were able to time each stimulus when presented separately. However, when both stimuli were presented simultaneously, rats with NBM lesions were able to time only a single stimulus. Thus, these rats demonstrated an impairment of divided attention. The data obtained with lesions to the NBM were qualitatively similar to those from animals given lesions of the frontal cortex suggesting that the NBM projections

to the frontal cortex may be important in divided attention.

Because expectancy can influence attention, the present study examined the role of the NBM in expectancy using the two-choice reaction time task described previously. A heterogeneous population of cells is located in the NBM. The two major types of cells use acetylcholine and GABA as their transmitters. Both of these major cell populations project to the cortex. The GABAergic cells of the NBM project mainly to cortical interneurons. The cholinergic neurons of the NBM project to both the principal cells of the cortex and the interneurons. The anatomical and physiological data suggest that the NBM may be important in modulating cortical function.

The activity of NBM neurons was altered by infusing muscimol, a GABAergic agonist, into the NBM. Expectancy was altered by varying relative stimulus probability. Reaction time, percentage of errors, discriminability, and response bias were measured as before.

For surgery, atropine methyl nitrate (0.2 mg/kg) was administered to each rat one hour prior to surgery. Surgical anesthesia was achieved using sodium secobarbital (50 mg/kg, i.p.) with supplements given as needed throughout surgery. A Deltaphase isothermal pad (BrainTree Scientific, Inc.) maintained the body temperature of the rat during surgery.

The end of a guide cannula was placed 2 mm above the substantia innominata of each NBM at 0.8 mm posterior and 2.6 mm lateral to bregma and 4.8 mm ventral from the surface of the brain. Each guide cannula was a stainless steel tube, 26 gauge, 10 mm long. The guide cannula was fixed to the skull and jeweler's screws with dental cement. A stylet was constructed from an 11 mm piece of 32 gauge stainless steel tubing, bent at a 90° angle 9 mm from the tip. The stylet was inserted into the guide cannula after the surgery. Each rat was allowed 2 days to recover from surgery before behavioral training was continued. The first infusion took place 1 week following surgery.

Muscimol, a GABA agonist, was infused simultaneously into both NBM. Each injector was constructed from 32 gauge stainless steel tubing, bent at a 45° angle 12 mm from the tip, and connected to PE-10 tubing. Each tube was attached to a 10 μ l Hamilton syringe. Both syringes were attached to an Orion syringe pump that delivered fluid at a rate of 0.1 μ l/min. Each injector was inserted into a guide cannula immediately before infusion. The tip of the injector extended 2 mm beyond the tip of the guide cannula and into the NBM. Muscimol (0.5, 1, or 2.5 nanograms) was infused during 5 minutes (0.1 μ l/min). During the infusion, the rat was free to move about the recording box. The injectors were left in place an additional minute following the infusion.

The test session, 45 minutes long, started 5 minutes after the end of an infusion. Infusions of muscimol occurred twice a week with a minimum of 2 days between infusions. The remaining sessions were used to obtain uninfused control data.

At the end of the study, secobarbital was used to anesthetize the rat. Chicago Sky Blue dye was infused ($0.1 \mu\text{l}/\text{min}$ for 5 minutes) through an injector to verify the location of the drug infusions. Transcardial perfusion was performed with saline, followed by 10% formalin solution. The brain was removed, soaked in 10% formalin, and subsequently placed in 20% sucrose-formalin for several days. Tissue sections ($50 \mu\text{m}$) were cut coronally on a cryostat and stained with neutral red. In 9 rats, the infusion was confined to the NBM, and the data from these rats were used in the behavioral analysis.

For visual stimuli, stimulus probability altered reaction time, so that increasing stimulus probability decreased reaction times. Muscimol increased reaction time in a dose-dependent manner. The medium and high concentrations of muscimol (1 and 2.5 nanograms) significantly increased reaction time compared to baseline conditions in which no infusions were given. The lowest dose of muscimol (0.5 nanograms) was not significantly different from reaction time in the baseline condition. No interactions of muscimol and stimulus probability were observed for reaction time.

For auditory stimuli, stimulus probability did not alter reaction time. Muscimol increased reaction times in a dose-dependent manner. Muscimol at all doses significantly increased reaction times to the auditory stimulus. As in the case for reaction time to visual stimuli, muscimol and stimulus probability did not interact significantly.

Increasing stimulus probabilities decreased the probability of an error. Errors to lights and tones were similar. Muscimol significantly increased the probability of an error. Because our previous study demonstrated differences in the probability of an error for lights and tones, responses to each of these stimuli were analyzed separately.

For lights, increasing probability decreased the probability of an error. Muscimol did not increase the probability of an error on light trials. Drug dose and stimulus probability did not interact for probability of a correct response.

For tones, stimulus probability significantly altered the probability of an error. Increasing the probability of a tone decreased the percentage of errors. Muscimol did not alter the probability of an error. Muscimol and stimulus probability did not interact for the probability of an error.

Discriminability was calculated for all sessions in which a choice between two stimuli were possible. Thus, the 100% light and 100% tone sessions were not included in this analysis. Stimulus probability altered discriminability; increasing probability of light trials increased discriminability. Muscimol significantly decreased discriminability in a dose-dependent manner. The highest dose of muscimol (2.5 nanograms) decreased discriminability compared to that observed in the baseline condition. Muscimol and stimulus probability did not interact for discriminability.

Response bias was shifted toward the more frequent stimulus. Muscimol did not alter response bias compared to baseline conditions.

The data in this study replicate our previous results in which stimulus probability influenced the probability of an error for both stimuli and reaction time to the visual stimulus. Similar to our previous results, reaction time to the auditory stimulus was not altered by stimulus probability. Bias was shifted towards the more frequent stimulus.

Muscimol increased reaction time for both stimuli, and decreased discriminability, but did not alter the probability of an error or response bias. Muscimol produced main effects for these measures but did not interact with stimulus probability. The change in discriminability suggests that muscimol in the NBM may interfere with perceptual and additional processes. The absence of an effect on response bias suggests that it did not interfere with response processes.

This pattern of results indicates that muscimol infusion into the NBM altered the attentional mechanisms involved in discriminability, but not other cognitive processes such as those involved in basic sensory input, response output, and long-term memory. Other analyses suggest that the NBM may be most important for the disengagement/shift function in divided attention.

Previous results have suggested a role of the NBM in attentional processes. Lesions of the NBM with ibotenic acid impaired divided attention but not focussed attention. Rats were trained in a temporal discrimination in which two stimuli signalled different fixed intervals. Each trial presented either a single stimulus or both stimuli simultaneously. Trials with a single stimulus assessed focussed attention, and trials with both stimuli presented simultaneously assessed divided attention. Normal rats were able to time each stimulus accurately whether presented alone or together with the second stimulus. Thus, normal rats had accurate focussed attention and divided attention. Rats with lesions of the NBM accurately timed each stimulus when presented alone, demonstrating good focussed attention. However, they were not able to accurately time the stimuli when presented together, thus demonstrating an impairment of divided attention.

In summary, the present experiment demonstrates that the NBM is important in the speed and accuracy of responding in a choice reaction time task. The decreases in discriminability following infusions of muscimol into the NBM are consistent with the idea that the NBM plays an important role in attentional processes. Because inactivation of the cells in the NBM following muscimol infusions did not alter response bias, the results suggest that the NBM is not important in expectancy or response processes.